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STREAM AMPHIBIANS AS INDICATORS OF ECOSYSTEM STRESS: A CASE STUDY FROM CALIFORNIA'S REDWOODS

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Abstract. Road construction of the Redwood National Park highway bypass resulted in a large accidental infusion of fine sediments into pristine streams in Prairie Creek State Park, California, during an October 1989 storm event. This incident provided a natural experiment where we could measure, compare, and evaluate native stream amphibian densities as indicators of stream ecosystem stress. We employed a habitat-based, stratified sampling design to assess the impacts of these sediments on the densities of aquatic amphibians in five impacted streams by comparing them with densities in five adjacent, unimpacted (control) streams. Three species were sampled in numbers sufficient to be informative: tailed frogs (*Ascaphus truei*, larvae), Pacific giant salamanders (*Dicamptodon tenebrosus*, paedomorphs and larvae), and southern torrent salamanders (*Rhyacotriton variegatus*, adults and larvae). Densities of amphibians were significantly lower in the streams impacted by sediment. While sediment effects were species specific, reflecting differential use of stream microhabitats, the shared vulnerability of these species to infusions of fine sediments is probably the result of their common reliance on interstitial spaces in the streambed matrix for critical life requisites, such as cover and foraging. Many stream-dwelling amphibians are highly philopatric and long-lived, and they exist in relatively stable populations. These attributes make them more tractable and reliable indicators of potential biotic diversity in stream ecosystems than anadromous fish or macroinvertebrates, and their relative abundance can be a useful indicator of stream condition.

Keywords: Ascaphus truei; *bioindicators; California;* Dicamptodon tenebrosus; *ecosystem stress; redwood ecosystem;* Rhyacotriton variegatus; *sedimentation; stream amphibians.*

INTRODUCTION

The condition of the physical habitat is critically important in stream (lotic) ecosystems and can change more easily and quickly than in most other ecosystems (Power et al. 1988). Sedimentation of aquatic ecosystems is a common outcome of many land management activities, including timber harvesting, road building, mining, and grazing (Meehan 1991, Reid 1993, Waters 1995). Consequently, stress due to increased sedimentation is one of the most common causes of ecological dysfunction in lotic ecosystems (Waters 1995). The negative impacts of sediments on stream-dwelling organisms, including fishes, stream and benthic invertebrates, and periphyton, are well documented (Newcombe.and MacDonald 1991, Meehan 1991, Waters 1995). However, few studies have examined the direct effects of sediments on stream-dwelling amphibians (see Hall et al. 1978, Hawkins et al. 1983, Bury and Corn 1988, Corn and Bury 1989).

In the developing lexicon of ecosystem "health" (see Suter 1993 for a critique of the health analogy applied to ecosystems), there is consensus that "unhealthy" or stressed ecosystems manifest common symptoms of degradation (Godron and Forman 1983, Odum 1985, Steedman and Regier 1987). Among these symptoms of ecosystem dysfunction are: (1) alteration in biotic community structure to favor smaller life forms; (2) reduced species diversity, (3) increased dominance by *"r"* selected species, (4) incrcased.dominance by exotic species, (5) shortened food-chain length, (6) increased disease prevalence, and (7) reduced population stability (Rapport 1992). While stressed ecosystems do not always manifest all of the above symptoms, in the majority of cases, most do appear (Rapport et al. 1985). The major challenge in ecosystem diagnosis is to identify early warning signs of incipient pathology (Rapport 1992; Rapport and Regier 1995). Odum (1992) noted that "the first signs of environmental stress usually occur at the population level, affecting especially sensitive species" (see also Rapport and Regier 1995). Such sensitive species are obvious candidates for indicator species. The use of indicator species is fraught with pitfalls and must be based on precise definitions and procedures to be effective and credible (Landres et al. 1988). However, the approach of finding and monitoring early indicators of ecosystem stress has the advantage of shortening the relatively slow response time of the whole ecosystem to stress by shifting attention to the much quicker response time of sensitive species (Rapport 1992). Such indicators would ideally have the combined attributes

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of being holistic, early warning, and diagnostic (Rapport 1992). Furthermore, these indicators need to be abundant and tractable elements of the system whose natural perturbations can be distinguished from states indicative of ecosystem dysfunction.

Amphibians are thought to be sensitive to perturbations in both terrestrial and aquatic environments because of their dual life histories, highly specialized physiological adaptations, and specific microhabitat requirements (Bury 1988, Vitt et al. 1990, Wake 1990, Olson 1992, Blaustein -1994, Blaustein et al. 1994*a*, Stebbins and Cohen 1995). During their aquatic stages, many stream-dwelling amphibian larvae are highly specialized in their uses of lotic microhabitats for both foraging and cover. Such specialized adaptations can render them susceptible to even minor environmental changes that alter their ability to seek cover from predators and to forage for phytoplankton, zooplankton, insects, and other invertebrates. In lotic habitats these specializations are shared with early life stages of both anadromous and freshwater fishes, as well as many stream invertebrates. Amphibians are relatively long-lived compared with invertebrates and fishes (e.g., Moyle 1976, Groot and Margolis 1991). Daugherty and Sheldon (1982*a*) reported a tailed frog with a known age of 14 yr, and Hairston (1987) reported longevity records for six families of salamanders that ranged from 10 to 55 yr. Amphibians are also highly philopatric compared to most fishes (see Daugherty and Sheldon 1982*b*, Welsh and Lind 1992), can occur in relatively stable numbers (Hairston 1987), and are readily sampled. Thus, we believe they are potentially more trac--table and reliable environmental indicators than these other taxa. Few studies have been designed specifically to examine the responses of amphibians to environmental perturbations in aquatic ecosystems (but see Moyle 1973, Hall et al. 1978, Hawkins et al. 1983, Hayes and Jennings 1986, Corn and Bury 1989, Welsh 1990, Blaustein et al. 1994*b*). In this paper we report the results of a study of amphibian population responses to alterations of the physical habitat in streams due to abnormal infusions of fine sediments and evaluate the use of amphibians as indicators of stream ecosystem dysfunction.

The primary challenge with indicator species, or any study where causal arguments are being made about shifts in presence or abundance, lies in separating any natural fluctuations in numbers from those attributable to anthropogenic environmental stresses (Pechmann et al. 1991, Blaustein 1994, Blaustein et al. 1994*b*, Pechmann and Wilbur 1994). The coast redwood (*Sequoia sempervirens*) ecosystem (Zinke 1977) where our study was conducted is self-perpetuating and in a late-seral or old-growth stage (i.e., in a steady state; Bormann and Likens 1979; see also Franklin and Hemstrom 1981, Veirs 1982). Based on the resistance-resilience model of ecosystem stability (Waide 1995), the coastal redwood ecosystem is among the most stable on the planet, and even the relatively dynamic lotic environment (Power et al. 1988) within late seral redwood forest is comparatively stable. Contrasting the potential life-spans of the native amphibians relative to that of the trees that define this ecosystem, it is certainly a highly stable environment from the perspective of the amphibians. We believe that it is reasonable to assume that in such a stable system, natural population perturbations within the amphibian assemblage would be minimized, and marked changes in their numbers over a short period of time could confidently be considered an indication of ecosystem dysfunction. Even with metamorphosis and the consequent movement of individuals from aquatic to terrestrial environments, populations of long-lived species with multiyear larval periods would remain relatively stable. Any pulses of newly hatched larvae entering the system could easily be accounted for in analysis by removing the first year class if that were appropriate given the question being addressed. While we can offer no direct evidence from the Pacific Northwest in support of our assumption of stable amphibian populations in stable environments, there are relevant data from forested ecosystems of the eastern United States. Hairston (1987) indicated that stream salamander populations from the Appalachian Mountains (*Desmognathus* spp.) have remained stable for up to seven years (length of time studied). He also reported stable populations in pond and terrestrial environments (see also Hairston and Wiley 1993), and concluded that salamander populations are apparently minimally affected by stochastic events, unless these events are destructive of the habitat (Hairston 1987).

A combination of natural and anthropogenic events during the fall of 1989 created a natural experiment, which afforded us an opportunity to test the response of amphibians to ecosystem stress in streams of an old-growth redwood ecosystem. The Redwood National Park bypass project was a large highway construction project adjacent to the eastern border of Prairie Creek Redwoods State Park, Humboldt County, California. This area received >12.7 cm of precipitation during a major storm 20-23 October 1989, which resulted in large infusions of sediments from the ongoing road construction into seven stream channels in the Prairie Creek drainage. The fine sediment layer deposited on affected streambeds measured 0.3-5.0 cm in depth (Anonymous 1991).

Here we provide an analysis of the effects of this combination of shallow mass wasting and surficial erosion (hereafter the erosion event) on densities of the three most abundant native, stream-dwelling amphibians in five of these streams. Our approach was to examine and compare these densities with those of the same species in five unimpacted (control) streams in the same basin. We also examined fine-scale microhabitat relationships within the unimpacted streams to help interpret any differences in amphibian numbers

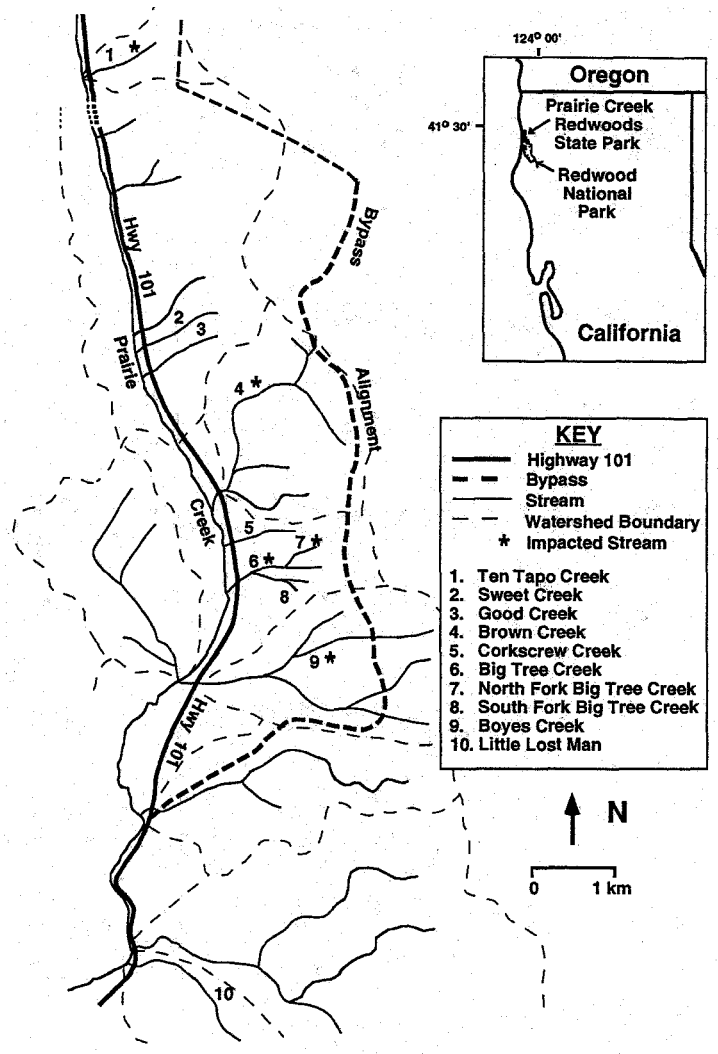

FIG. 1. Locations of impacted (*) and unimpacted streams in Prairie Creek State Redwoods and Redwood National Park, Humboldt County, California. All drainages were sampled for amphibians from June through August 1990. (Modified from Welsh et al. 1997.)

that might be revealed between the impacted and unimpacted sets of streams.

Site and species accounts

For our study of the impacts of the erosion event on the amphibian community we selected the five of seven streams affected by the event that drained westward into Prairie Creek (Anonymous 1991). Our five control streams were selected from those unimpacted streams in the same drainage, with a similar westward aspect, that were interspersed among the impacted streams (Fig. 1). The two sets of streams (five unimpacted and five impacted) were of similar size and orientation, and vegetative cover. Of the total set of 10 streams, nine were located within Prairie Creek Redwoods State Park and one control stream (Little Lost Man Creek) was located in the same drainage basin in adjacent Redwood National Park (Fig. 1).

Three species of amphibians were sufficiently abundant in these streams to enable our study.

Pacific giant salamander.-The larval and paedomorphic forms of this salamander 'are strictly aquatic and general accounts of their habitat describe them as bottom dwellers in mountain streams, lakes, and ponds (Nussbaum et al. 1983, Leonard et al. 1993) where they are often found under cobble-size substrates (Parker 1991, Welsh 1993). This salamander can be extremely abundant in small streams of the Pacific Northwest, accounting for as much as 99% of the predator biomass in such systems (Murphy and Hall 1981, Hawkins et al. 1983). Larvae of this species typically require two complete summers of growth before metamorphosis occurs (Leonard et al. 1993).

Tailed frog.-Welsh (1993) summarized the niche for the larval tailed frog as ". . . clear, cool, fast-flowing streams in coniferous forests of the Pacific Northwest." Conditions within streams with larvae ". . . consisted of fast current over coarse gravel, pebble, cobble, or boulder substrates, with little fine sediment" (Welsh 1993). These conditions included intermediate to high water velocity and cold water temperatures (Welsh 1990, 1993; see also H. H. Welsh and A. J. Lind,

unpublished manuscript). The strong association with fast-flowing, cold water habitats probably reflects the evolutionary history of this frog (sensu Holt 1987). Tailed frogs are unique among temperate anurans in being specifically adapted to these unusual and extreme conditions (cf. deVlaming and Bury 1970, Gradwell 1971, Claussen 1973, Brown 1975). Larvae from lowland populations of the tailed frog typically require 1-2 yr before metamorphosis occurs (Leonard et al. 1993).

Southern torrent salamander.-General descriptions of the habitat of this small, secretive salamander indicate that it occurs in and along small streams, spring heads, and seepages (Anderson 1968, Nussbaum and Tait 1977, Nussbaum et al. 1983, Good and Wake 1992, Welsh 1993, Welsh and Lind 1996). Larval individuals can be found in the loose substrates of small streambeds. Adults are both stream and streamside dwellers, occurring where water flows through a matrix of unsorted rock substrates (J. Baucom, *personal communication).* Typical habitats include the splash zones of rocky tumbling brooks and waterfalls. Adults often occur side-by-side with larvae within coarse substrates in streams (Welsh and Lind 1992, 1996). The southern torrent salamander has a four and one-half to five year larval period (Leonard et al. 1993).

METHODS

From June to August 1990, we sampled five impacted (subjected to a mass sediment infusion) and five unimpacted streams. Our study design assumed that amphibian community composition and densities in the unimpacted streams resembled the composition and densities present in the impacted streams had the erosion event not occurred. The similarities and proximity of these 10 streams, the stability of the coast redwood ecosystem, and the lack of any documented historical perturbations that impacted any of these streams prior to the highway construction project, all support this assumption. We alternated sampling between impacted and unimpacted streams to ameliorate the effects of any recruitment of newly hatched larval amphibians on the density estimates. In addition, we tested the supposition that the two stream sets were geomorphically similar (see *Methods: Comparisons* of *physical habitat).*

Habitat typing of streams

Our sampling design was stratified by mesohabitat type (e.g., pool, run, riffle, and other types; Welsh et al. 1997). Prior to sampling for amphibians, each stream was mapped from Highway 101 east to its headwaters (Fig. 1). The mapping included the subdivision and classification of streams at the level of geomorphological reach type (braided, alluvial, or confined) and stream mesohabitat composition (Appendix).

Comparisons of physical habitat in unimpacted and impacted streams

We lumped similar mesohabitat types into five composite categories (after Hawkins et al. 1993), in order to increase sample sizes and simplify analyses: (1) all pools, including main channel, backwater, and secondary channel pools; (2) glides and runs; (3) riffles; (4) step runs; and (5) step pools. These five categories are hereafter referred to as the primary mesohabitat types (Appendix).

In order to insure that any differences in amphibian densities detected between the unimpacted and impacted streams could not be attributed to. differences in stream reach type (alluvial, braided, or confined) or differences in the composition of primary mesohabitat types, we tested for differences in these parameters between the two stream sets. We performed unpaired Student's t tests (Zar 1995) of the mean proportions of stream length by reach type and primary mesohabitat type for each set of streams. The significance level (α) was set at 0.05 with a Bonferroni adjustment (Stevens 1986) applied for multiple tests (a for mesohabitat type tests = 0.01; α for reach type tests = 0.017).

To evaluate sediment loads in each stream we sampled the pool mesohabitats where fine sediments (<2 mm) tend to collect (Lisle and Hilton 1992). Fine sediment depths were measured at three locations in each pool bowl (the upstream end, the middle, and at the downstream end) (Appendix), with the three measurements averaged for analysis. We also visually estimated the percentage of embedded coarse substrate at the pool tail (Appendix). The two pool sediment variables were employed to evaluate differences in fine sediments between the two sets of streams but were not used in the analyses of amphibian densities. Unpaired Student's t tests were used to test differences in the mean sediment depth and the mean percentage of pool tail substrate embedded for each set of streams ($\alpha = 0.05$).

Amphibian sampling

Stream habitats for amphibian sampling were selected using a random systematic design based on stream length and ratios of primary mesohabitat types along each stream (Welsh et al. 1997). Working from west to east (upstream) and beginning at Highway 101 (Fig. 1), we sampled the first unit of every mesohabitat type encountered, then a randomly selected unit of each type between the second and the sixth, then every fifth unit of each type thereafter. This provided a proportional sampling effort of each mesohabitat type relative to its availability in each stream.

Within each selected stream mesohabitat unit, we systematically placed one or more amphibian sampling units (cross stream belt transects) based on habitat length, placing one belt transect for every 10 m of habitat (Fig. 2). Belt transects (hereafter belts) were 0.6 m wide and extended from bank to bank so that

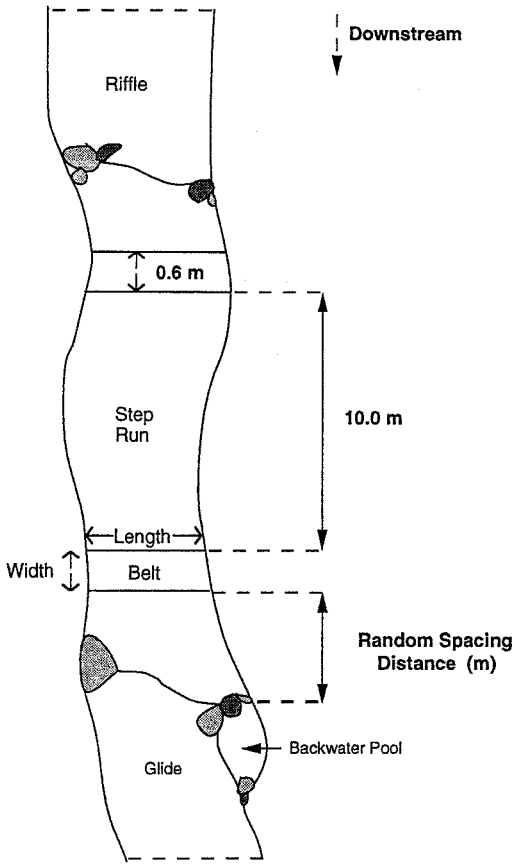

FIG. 2. Schematic representation of random-systematic belt placement within selected mesohabitats (see *Methods: Amphibian sampling).* Modified from Welsh et al. (1997).

sampling unit length varied with stream width. The length of each mesohabitat unit was divided by the total number of belts desired (approximately one every 10 m) to determine exact spacing, and a random distance between 0 and 10 m was used to determine placement of the first belt (Welsh et al. 1997). Each belt was then thoroughly searched for amphibians. The area was first scanned for visible animals and then all cover objects were removed working from bank to bank and upstream until the entire area was searched. Animals were captured using a metal mesh net, identified, sexed (if possible), measured (snout-vent and total length), and released after sampling was completed. Cover objects were returned to their original positions. We are confident that our searches captured all amphibians present in the open, and probably most of those under the first layer of large substrate (>16 mm diameter).

Three species were detected and sampled in numbers sufficient for statistical analyses: larval and paedomorphic (animals with larval morphology and sexual maturity) Pacific giant salamanders (*Dicamptodon tenebrosus*), *larval* tailed frogs (*Ascaphus truei*), and larval and adult southern torrent salamanders (*Rhyacotriton variegatus*). We did not differentiate larval and paedomorphic Pacific giant salamanders, and they were combined for analysis. Only six adult tailed frogs were captured. Because of this small sample and their primarily terrestrial habitat associations, they were omitted from the analyses. Four adult torrent salamanders were found, and because they occur in the same aquatic microhabitats as the larvae, the two life stages were combined for analyses. Histograms of snout-vent length indicated that our sampling occurred after the recruitment of Pacific giant and southern torrent salamander larvae, and before the recruitment of tailed frog larvae to our stream set.

Biotic and abiotic measurements associated with amphibian sampling

In order to characterize fine-scale or microhabitat attributes associated with amphibian captures, we estimated or measured 28 microhabitat parameters associated with the individual belt samples (Fig. 2) (Appendix: microhabitat attributes).

Statistical analyses

We used Statistical Analysis System (SAS version 6.12; SAS Institute 1997) to conduct all data analyses. In contrast to the stricter a = 0.05 used in testing for differences in geomorphology and pool fine sediment levels among the sets of streams, we set $\alpha = 0.10$ for our analysis of variance (ANOVA), analysis of covariance (ANCOVA), and correlation analysis. This moderate a provides a criterion more appropriate for the detection of ecological trends and it increases statistical power (Toft and Shea 1983, Toft 1991) (see Schrader-Frechette and McCoy [1993] for a thorough justification and evaluation of this methodological approach in ecology). Dependent variables were natural log-transformed, and some independent variables were arcsine-transformed, to meet the assumptions of normality and homogeneity of variance.

Analysis of variance.-We used partial hierarchical ANOVA to test for differences in densities of each amphibian species (the dependent variables) between impacted and unimpacted streams. Within each impact category (impacted and unimpacted) there are five streams, and within those streams five mesohabitat types are possible. This method permits us to partition the total variability into three components while adjusting for unequal sample sizes within the different levels. The unit of analysis was the mesohabitat unit (i.e., mesohabitat types within streams within impacts). The effect for impact was calculated using streams within impact as the mean square error (MSE). The effects for mesohabitat type and impact by mesohabitat type interaction were calculated using mesohabitat type within stream within impact as the MSE. The mean squares were calculated using Type I sums of squares (ss) as all mesohabitats were sampled in proportion to their occurrence in the population (Milliken and Johnson 1984). This was not the case with the overall model

F; thus it was not used to determine model significance. The following null hypotheses were tested:

H_{0_1} : There are no significant differences between impact and no impact for any of the three species;

H_{0_2} : There are no significant differences among mesohabitat types for any of the three species;

H_{0_3} : There is no interaction between mesohabitat type and impact for any of the three species.

When ANOVA provided evidence of differences among mesohabitats, we used Tukey's studentized multiple range test to compare the means.

Analysis of covariance.—In order to more closely examine the effects of specific fine sediment parameters (Appendix: fine aquatic substrates) on individual species we employed ANCOVA. We used this method to look for evidence of other possible effects of the erosion event that were not measured during our sampling (e.g., chronic suspended sediment load, bed instability) that may be indirectly related to sediment transport. This allowed us to adjust the ANOVA models by each fine sediment variable measured (Appendix). The model structure for the ANCOVA is the same as that of the ANOVA described (partial hierarchical) and employed Type I ss. The following null hypotheses were tested:

H_{0_1} : There are no significant differences between impact and no impact for any of the three species, when densities are adjusted by each of the fine sediment covariates;

H_{0_2} : There are no significant differences among mesohabitat types for any of the three species, when densities are adjusted by each of the fine sediment covariates;

H_{0_3} : There are no significant differences for the interaction of mesohabitat type and impact for any of the three species, when densities are adjusted by each of the fine sediment covariates.

The five fine sediment parameters consisted of two visual estimates of substrate composition, one estimate of substrate condition, and two measures of fine sediment derived from grab samples collected immediately adjacent and upstream of the belts (Appendix: fine aquatic substrates). In order to simplify the ANCOVA by eliminating redundancy among closely related variables, we used correlation analysis to select one variable from those pairs that described a similar parameter (percentage fines and silt volume, $r = 0.466$, $P < 0.0001$; percentage sand and sand volume, $r = 0.303$, $P < 0.0001$). From each of these pairs we chose the variable with the highest correlation with our dependent variables (percentage fines), or if the significant *r* values were equivocal relative to the dependent variables, we chose the measured variable (sand volume).

Significant covariates were determined using Type III sums of squares. Only those ANCOVA results with a reduced error variance for our tests were meaningful. Consequently, only those models with a decreased overall MSE were evaluated further. ANCOVA models that failed to reduce the MSE over the ANOVA or had a nonsignificant *F* for the covariate, failed to explain additional effects beyond those detected in the ANOVA.

Correlation analysis.-We performed correlation analyses of 28 microhabitat attributes measured or estimated within each belt sample (Appendix). We restricted this analysis to those data from belts in the control streams with captures of each of the three species in order to address the question "what measured or estimated microhabitat variables best characterized the fine-scale ecological relationships of the resident amphibians under pristine stream conditions?"

RESULTS

Comparisons of physical attributes between impacted and unimpacted streams

We surveyed and habitat typed 3.6 km of impacted streams and 3.2 km of unimpacted streams (Fig. 1). Comparisons of mean proportions of stream length by reach type and primary mesohabitat type indicated that there were no significant differences between the impacted and unimpacted sets of streams (Table 1). Assuming that the relative amount of available habitat is a reasonable indicator of the number of organisms that may be supported there (Southwood 1977, 1988), we consider that this lack of difference in geomorphological composition supported our assumption that the amphibian assemblages in the two sets of streams probably would have had similar species composition and densities had the erosion event not occurred.

Mean fine sediment (<2.0 mm) depths in the impacted pools ranged from 0.1 to 25.0 cm compared with 0.0-4.0 cm in the unimpacted pools (Fig. 3). Percentage embeddedness of pool tails ranged from 10 to 100% in the impacted streams and from 0 to 85% in the unimpacted streams. Tests between the two sets of streams for both the mean sediment depth in pool bowls, and the percentage of substrate embeddedness at the pool tails, showed significantly greater amounts of sediment in the impacted streams (Fig. 3). This clearly demonstrates an impact effect of the 1989 erosion event still remained when we sampled in 1990.

Comparisons of amphibian densities between impacted and unimpacted streams

We sampled a total of 267 belts in 179 mesohabitat units, with 93 habitat units (137 belts) in the impacted streams and 86 habitat units (130 belts) in the unimpacted streams. We captured a total of 540 amphibians; larval and paedomorphic individuals of the Pacific giant salamander were the most common ($n = 296$), followed by larval tailed frogs ($n = 205$), and larval and adult southern torrent salamanders ($n = 39$).

Analysis of amphibian densities.-Densities of the three species varied by mesohabitat type and impact (Fig. 4). The Pacific giant and southern torrent salamanders showed significant differences for impact

TABLE 1. Comparison of reach types and mesohabitat composition for 10 streams sampled for aquatic amphibians in Prairie Creek Redwoods State Park and Redwood National Park, Humboldt County, California, 1990.

	Reach types			Mesohabitat types				
Stream	Alluvial	Braided	Confined	All pools	Glide/run	Riffle	Step run	Step pool
Unimpacted streams								
Corkscrew	0	0	100.0	5.3	2.0	41.5	9.7	41.5
Good	0	67.7	32.3	4.4	5.6	40.6	46.2	4.2
Little Lost Man	67.7	0	32.3	7.6	1.4	3.4	37.0	51.1
S. fork Big Tree	0	0	100.0	10.8	6.2	14.9	0.0	68.1
Sweet	0	3.2	96.8	3.0	0.7	36.6	39.1	21.0
$\bar{x}$	13.5	14.2	72.3	6.2	3.2	27.4	26.4	37.2
	(14.0)	(13.0)	(16.0)	(1.4)	(1.1)	(7.7)	(9.1)	(11.0)
Impacted streams								
Big Tree	6.0	27.7	66.3	20.6	3.9	19.3	11.4	45.6
Boyes	84.9	15.1	0	19.9	4.8	19.6	30.2	18.0
Brown	0	0	100.0	26.2	8.5	20.7	22.0	24.3
N. fork Big Tree	0	20.2	79.8	3.7	0.0	12.0	4.2	80.2
Ten Tapo	81.9	18.1	0	18.0	0.0	14.7	12.2	56.4
$\bar{x}$	34.6	16.2	49.2	17.7	3.4	17.3	16.0	44.9
	(20.0)	(4.6)	(21.0)	(3.7)	(1.6)	(1.7)	(4.6)	(11.0)
t	–0.87	-0.14	0.87	-2.88	-0.12	1.29	1.03	-0.48
P†	0.41	0.89	0.41	0.02	0.91	0.27	0.33	0.64

Note: Percentage of stream length by reach and mesohabitat type, mean, and standard error (in parentheses) are reported. Comparisons of impacted and unimpacted streams were made using Student's t.†

† Significant t probability values were interpreted using a Bonferroni adjustment (Stevens 1986).

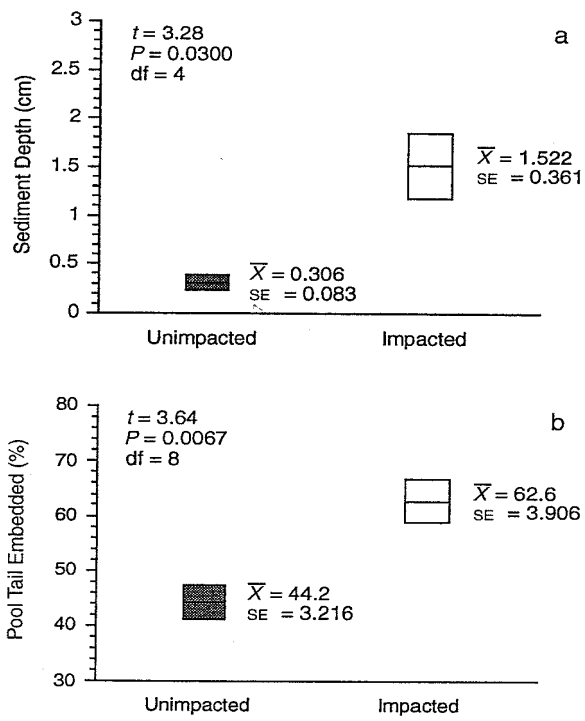

FIG. 3. Comparisons of sediment depths (a) and pool tail embeddedness estimates (b) in impacted and unimpacted streams. Boxes indicate means (from three measures of sediment depth [cm] along the central axis at the top, middle, and bottom of each pool bow), ± 1 SE.

(sedimentation); in all cases the densities in unimpacted streams were greater (Table 2a). The tailed frog and southern torrent salamander showed significant differences among mesohabitat types (Table 2a). There was also a significant interaction between impact and mesohabitat type for the tailed frog (Table 2a).

In the impacted streams, there were no significant differences among mesohabitat types for the Pacific giant and southern torrent salamanders. However, tailed frog density was significantly greater in riffles compared to pools (Table 2b). In the unimpacted streams tailed frog larvae showed strong habitat specialization and were significantly more abundant in both riffles and step runs compared with other mesohabitat types (Table 2b). The torrent salamander also occurred more often in riffle than pool habitat in the unimpacted streams (Table 2b), although there were no captures in pools, glides, or runs (Fig. 4). There were no differences in mesohabitat type for the Pacific giant salamander in the unimpacted streams (Fig. 4).

Effects of fine sediment attributes.-The Pacific giant salamander and tailed frog yielded significant covariate models (Table 3), indicating additional variation was explained beyond the ANOVA. For these same depen dent variables, percentage embedded caused the great est reduction in variability (Table 3). In the models that were adjusted for percentage embedded, there were no significant differences detected with respect to impact (the first hypothesis test) for the Pacific giant sala mander, or the tailed frog, indicating that once the data were adjusted for this covariate no further differences could be explained (Table 3a, b).

With respect to percentage embedded. the Pacific

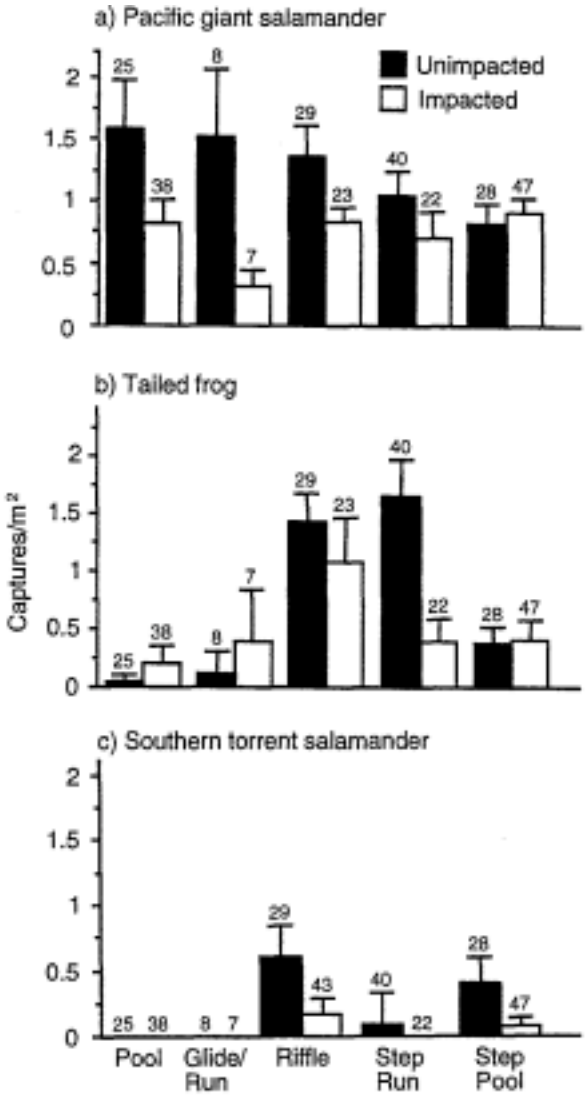

FIG. 4. Densities, of three species of amphibians are shown with respect to impact and mesohabitat type. Bars represent means (and one standard error) for the stream sets (five streams in each). Numbers over bars are belts sampled.

giant salamander showed no differences for mesohabitat type or the interaction (Table 3a). In the model adjusted for percentage embedded, the tailed frog showed significant results in the tests for mesohabitat type and its interaction with impact, indicating that additional sediment effects were influencing the system beyond those explained by the ANOVA (Table 2) and the adjustment for percentage embedded (Table 3b).

The Pacific giant salamander had one additional significant covariate, percentage fines. As with percentage embedded above, no significant differences were found in the tests (Table 3a). There were no other significant covariate models for any of the three species (Table 3).

Correlation analyses of microhabitat attributes.-Of the 28 microhabitat parameters we examined, 14 were significantly correlated with amphibian density (Table 4). Nine attributes were correlated with Pacific giant salamander density, two attributes were correlated with tailed frog density, and five attributes were correlated with southern torrent salamander density (Table 4). The two salamander species responded differently to flow rates within belts. The Pacific giant salamander densities were lower in areas of high flow, while southern torrent salamander densities increased with flow rate (Table 4). Pacific giant salamander density increased in belts with larger amounts of woody debris cover, while southern torrent salamander density declined in association with both wood cover and substrates (Table 4).

DISCUSSION

Our study indicated that the stream amphibian community was negatively impacted by the erosion event caused by the bypass construction and the October 1989 storm (Table 3, Fig. 4). Our analysis indicated that this response differed considerably by species (Table 3). For example, the ANCOVA model for the Pacific giant salamander suggests that it is less sensitive than the other species to fine sediments (Table 3), but it was negatively associated with sand (Table 4). Our ANCOVA results for the tailed frog (Table 3) suggested that the impact of the erosion event acted at the level of microhabitat within streams and consisted primarily of fine particles restricting access to the streambed matrix (i.e., percentage embedded) (cf. Lisle 1989, Lisle and Lewis 1992). However, the significant results for both mesohabitat type and the interaction effects (Table 3) indicated that additional factors may be affecting the tailed frog. For the Pacific giant salamander and the tailed frog, we found significant positive associations with relatively coarse substrates (e.g., cobble; Table 4), where matrix interstices can be reduced or eliminated by fine sediments (i.e., percentage embedded).

Pacific giant salamander

The Pacific giant salamander was the least habitat specific, showing no clear association with any particular stream mesohabitat type (Fig. 4, Table 3). As a habitat generalist, this species is most likely affected by sedimentation across all stream mesohabitat types, but probably more so in pools where fine sediment accumulation is greatest (Lisle and Hilton 1992).

Analysis of substrate associations indicated that higher relative amounts of gravel and cobble were the best predictors of Pacific giant salamander abundance (Table 4; H. H. Welsh and A. J. Lind, *unpublished manuscript).* This outcome underscores the relative importance of coarse, rocky substrates, which have a high relative amount of interstitial space (see also Welsh 1993). Parker (1991) experimentally demonstrated the importance of cobble-size substrates as cover for larval Pacific giant salamanders in pool habitats in a stream similar to ours in northwestern California. Concomitantly, we found fewer salamanders in areas with great-

TABLE 2. (a) Partial hierarchical analysis of variance (ANOVA) of three amphibian species by impact (presence or absence of fine sediment infusion), stream number, and mesohabitat type, and (b) Tukey pairwise comparisons of mesohabitat types.

a) ANOVA results

Factor	df	MSE	*F*	*P*	Result
Dependent: Pacific giant salamander					
Overall model	46,132	0.2799	0.96	0.5588	
Tests					
Impact	1,8	1.5010	3.95	0.0820	U >I†
Mesohabitat type	4,29	0.2932	1.58	0.2050	NS
Impact X Mesohabitat type	4,29	0.3058	1.65	0.1881	NS
Dependent: Tailed frog					
Overall model	46,132	0.1803	2.72	0.0001	
Tests					
Impact	1,8	0.9252	2.06	0.1888	NS
Mesohabitat type	4,29	2.2925	11.38	0.0001	
Impact X Mesohabitat type	4,29	0.7507	3.73	0.0145	
Dependent: Southern torrent salamander					
Overall model	46,132	0.0568	2.78	0.0001	
Tests					
Impact	1,8	0.7982	4.93	0.0572	U > I†
Mesohabitat type	4,29	0.3144	2.67	0.0519	
Impact X Mesohabitat type	4,29	0.1258	1.07	0.3896	NS

b) Tukey pairwise comparison results*

Pacific giant salamander	Comparison: Mesohabitat type (with respect to Impact)				
Impacted streams	Glide/run	Step Pool	Pool	Step Run	Riffle
Unimpacted streams	Step Pool	Riffle	Glide/Run	Pool	Step Run
Tailed frog	Comparison: Impact X Mesohabitat type				
Impacted streams	Pool	Glide/Run	Step Run	Step Pool	Riffle
Unimpacted streams	Pool	Glide/Run	Step Pool	Riffle	Step Run
Southern torrent salamander	Comparison: Mesohabitat type (with respect to Impact)				
Impacted streams	Pool	Step Run	Glide/Run	Step Pool	Riffle
Unimpacted streams	Pool	Glide/Run	Step Run	Step Pool	Riffle

† U = unimpacted streams, I = impacted streams.

‡ Amphibian mean density increases from left to right; lines indicate nonrejecting subsets.

er volumes of sand (Table 4), a condition that limits available interstitial spaces (see also Hall et al. 1978, Murphy and Hall 1981, Murphy et al. 1981, Hawkins et al. 1983, Corn and Bury 1989). However, none of the fine sediment variables alone could explain the significant differences we saw in giant salamander abundances with respect to impact (Table 2, Table 3). Because giant salamanders use more available stream mesohabitat types (Fig. 4), it is possible they are better able to compensate for habitat loss resulting from sedimentation (Table 2). Such adjustments might involve changing habitat use patterns or even modifying preferred sites by excavating sediments as has been seen with an ambystomatid salamander (e.g., Jennings 1996), but these hypotheses are currently untested.

Tailed frog larvae

Tailed frog larvae were the most specific in habitat use, showing a strong association with step runs and riffles vs. step pools and all other stream mesohabitat types (Fig. 4). They also demonstrated a strong association with coarse substrates (cobble) (Table 4; see also Nussbaum et al. 1983, Welsh 1993; H. H. Welsh and A. J. Lind, *unpublished manuscript).* Coarse substrates provide the interstitial space important for cover from both predation and high winter stream flows (e.g., Metter 1963, 1968), as well as providing abundant surface area for diatom production, an important food source. Fast-water habitats are less prone to trapping sediment due to the higher, more uniform velocity of water (Lisle and Hilton 1992). However, results for the tailed frog showed a significant interaction between sediment impact and mesohabitat type (Table 3). This indicated that tailed frog larvae were adversely impacted even in those high velocity habitats that are likely to have lower sediment loads (Fig. 4). This result suggests that something other than sediment filling the interstices was affecting tailed frog abundances in impacted streams. Sediment may impact critical food resources, both in adjacent lower gradient areas and in those mesohabitats occupied by tailed frog larvae. When we examined data from across all streams, we

TABLE 3. Partial hierarchical analysis of covariance of three species by impact (presence or absence of sediment), stream number, and mesohabitat type. The covariates were sediment variables taken in association with animal sampling.

Factor	df	MSE	*F*	*P*
a) Dependent: Pacific giant salamander				
i) Overall model	47, 130	0.268	1.11	0.3127
Covariate: Percentage embedded	1,8	1.812	6.75	0.0105†
Tests				
Impact	1,8	0.071	0.19	0.6718
Mesohabitat type		4, 29	0.346	1.84 0.1484
Impact X Mesohabitat type	4, 29	0.313	1.66	0.1860
ii) Overall model	47, 131	0.269	1.11	0.3199
Covariate: Percentage fines	1,8	1.711	6.36	0.0129†
Tests				
Impact	1,8	0.474	1.27	0.2928
Mesohabitat type	4, 29	0.311	1.61	0.1984
Impact X Mesohabitat type	4, 29	0.353	1.83	0.1510
iii) Overall model	47, 130	0.280	0.96	0.5512
Covariate: Sand volume	1,8	0.248	0.89	0.3476
b) Dependent: Tailed frog				
i) Overall model	47, 130	0.166	3.17	0.0001
Covariate: Percentage embedded	1,8	2.255	13.61	0.0003†
Tests				
Impact	1,8	0.519	1.34	0.2808
Mesohabitat type	4, 29	0.933	3.82	0.0129‡
Impact X Mesohabitat type	4, 29	0.720	2.95	0.0367‡
ii) Overall model	47, 131	0.178	2.75	0.0001
Covariate: Percentage fines	1,8	0.470	2.64	0.1065
iii) Overall model	47, 130	0.179	2.72	0.0001
Covariate: Sand volume	1,8	0.435	2.42	0.1219
c) Dependent: Southern torrent salamander				
i) Overall model	47, 130	0.058	2.69	0.0001
Covariate: Percentage embedded	1,8	0.024	0.41	0.5212
ii) Overall model	47, 131	0.057	2.71	0.0001
Covariate: Percentage fines	1,8	0.009	0.16	0.6881
iii) Overall model	47, 130	0.057	2.82	0.0001
Covariate: Sand volume	1,8	0.008	0.14	0.7119

Note: Test results are not reported for those models lacking a significant covariate.

†Covariate models with a significant model *F* using Type III ss and reduction in the MSE in the overall model over that of the ANOVA

‡Hypothesis tests with a significant effect detected using Type I ss after the covariate has been incorporated into the model.

found highly significant negative correlations between percentage of nonfila'rnentous algae and the three fine sediment variables used in our ANCOVA (percentage embedded, r = -0.572, P = 0.0001; percentage fines, r = -0.476, P = 0.0001; sand volume, r = -.393, P = 0.0001). Welsh (1993) reported that the amount of nonfilamentous algae (diatoms or periphyton) was a significant predictor of the presence and abundance of tailed frog larvae. Diatoms are the primary food for larval tailed frogs (Metter 1964, Nussbaum et al. 1983), so it follows that they would occur in greater abundance where periphyton is plentiful and avoid areas where it is sparse or absent. Even a thin layer of fine sediment can block sufficient light and inhibit the growth of algae (Newcombe and MacDonald 1991). During high flows greater amounts of sediment might scour algae off streambed substrates and thereby reduce periphyton biomass (Alabaster and Lloyd 1982).

Southern torrent salamander

The southern torrent salamander demonstrated intermediate mesohabitat specificity compared with the other two species examined. Southern torrent salamanders were absent from pools, and glides and runs. They occurred predominately in riffles, step runs, and step pools (Fig. 4). Thus, all of the mesohabitat types where they did occur were comprised primarily of moving and mixing waters. Even in these mesohabitats, southern torrent salamanders were found in higher abundance in the thalweg (main flow) and appeared to avoid mesohabitats composed primarily of margin (Table 4). This meso- and microhabitat specificity may be related to physiological constraints resulting from their specialized, reduced gill-arch system that restricts them to habitats that are characterized by cold, highly oxygenated water (i.e., mountain brooks, Valentine and Dennis 1964). The specific meso- and microhabitat associations of the southern torrent salamander could reflect a response to lower sediment loads in these habitats, but the lack of an interaction (Table 2) suggests that this habitat specificity is an ecological or evolutionary adaptation (Holt 1987) rather than a temporary response to adverse conditions. This species also ap

TABLE 4. Significant results of Pearson product-moment correlations are reported for 14 microhabitat variables (Appendix). Correlations were performed using stream belts with captures in unimpacted streams.

Variable	Pacific giant salamander†	Tailed frog‡	Southern torrent salamander§
Aquatic conditions			
Water temperature	-0.335	…	…
Proportion margin	…	…	-0.448
Flow thalweg	-0.282	…	0.311
Cover types			
Woody debris cover	0.318	…	-0.421
Riparian vegetation	0.197	…	…
Large rock cover	-0.383	…	…
Without cover	…	…	0.502
Coarse aquatic substrates			
Cobble	0.245	0.298	…
Large rock substrates	-0.437	…	…
Fine gravel volume	0.234	…	…
Woody debris substrates	0.273	…	-0.460
Fine aquatic substrates			
Embedded	…	-0.461	…
Fines	…	…	-0.654
Sand volume	-0.272	…	…

† Correlations with salamander density are based on 78 belts with salamander captures; correlations > 0.188 are significant at $P = 0.10$.

‡Correlations with tadpole density using 49 stream belts in the four primary mesohabitat types that had tailed frog captures (step runs, step pools, runs/glides, riffles); correlations > 0.238 are significant at $P = 0.10$.

§ Correlations with salamander density using 19 stream belts in the three primary mesohabitat types that had southern torrent salamander captures (step runs, step pools, and riffles); correlations > 0.389 are significant at $P = 0.10$.

peared to use areas lacking large cover objects (Table 4). We suspect that their avoidance of wood cover and substrates could be a means to elude predatory Pacific giant salamanders, which were often found associated with this cover type (Table 4). Stebbins (1953) and Nussbaum (1969) also speculated that Pacific giant salamander presence may restrict southern torrent salamander distribution.

The lack of a significant covariate model for the southern torrent salamander indicated that no further effects were detected over what was indicated by the ANOVA. However, the correlation analysis for this salamander showed a strong negative relationship with percentage fines (Table 4). Previous research also concluded that torrent salamanders are sensitive to fine sediments in, and substrate embeddedness of, the streambed matrix (Welsh 1993, Welsh and Lind 1996). Nonetheless, the southern torrent salamander may be able to compensate to some degree for the negative effects of sedimentation by favoring shallow stream microhabitats with steady flow where they occur in close association with cobble substrates (Welsh 1993, Welsh and Lind 1996). However, we cannot discount The possibility that the lack of an interaction effect may have resulted from the low number of belts with captures (10%) or high variability, which may have partially compromised our ability to detect differences.

In summary, our study indicated that sediment deposits from the October 1989 storm event had a negative effect on amphibian populations, with a pronounced effect on two out of three species examined. Furthermore, our ANCOVA results add new insight into the explanation for reduced abundances of tailed frog larvae based on sedimentation of interstices offered by Corn and Bury (1989). It appears that tailed frog larval abundances were reduced by some factor other than the direct impact of embeddedness, possibly as a result of the inhibition of periphyton growth, the scouring of that growth from streambed substrates, or both. Our results also documented differential use of stream mesohabitats by two of these species, and demonstrate how fine sediments can differentially affect stream amphibians in accordance with their particular meso- and microhabitat associations.

Amphibians as bioindicators

Results of our analyses are consistent with other studies that examined the habitat associations of these species at finer spatial scales and in ecosystems other than the redwoods (Murphy et al. 1981, Hawkins et al. 1983, Corn and Bury 1989, Bury et al. 1991, Parker 1991, Welsh 1993; H. H. Welsh and A. J. Lind, *unpublished manuscript).* Bury and Corn (1988) discussed the potential negative impacts of erosion events on stream amphibians of the Pacific Northwest. Such impacts have been documented for other stream systems in connection with timber harvesting activities and associated road building (Burns 1972, Beschta 1978, Rice et al. 1979, Reid and Dunne 1984, Chamberlin et al. 1991, Furniss et al. 1991). Corn and Bury (1989) documented differences in amphibian species richness and in the density and biomass of southern torrent salamanders, tailed frog larvae, and Pacific giant salamanders in logged vs. unlogged streams in southern Oregon. They attributed these declines to loss of critical microhabitat due to infusions of fine sediments. Populations of stream amphibians can be particularly sensitive to increased siltation because they frequent interstitial spaces among the loose, coarse substrates that comprise the matrix of most natural streambeds of the Pacific Northwest (Bury and Corn 1988, Corn and Bury 1989). Sedimentation fills these spaces, reducing available cover and foraging area and, undoubtedly, has similar impacts on other substrate-dwelling biota (cf. Lisle 1989, Lisle and Lewis 1992; see also Waters 1995).

As to the question of their applicability as bioindicators of environmental stress, we conclude that measuring and monitoring stream amphibian densities can provide a highly suitable and extremely sensitive barometer of ecological stress resulting from fine sedi

ment inputs, arguably one of the most pervasive stressors of lotic systems worldwide (Waters 1995). Other studies have indicated that the tailed frog and torrent salamander also show a marked sensitivity to another stressor in lotic systems, increased water temperature (Brattstrom 1963, deVlaming and Bury 1970, Claussen 1973, Welsh 1990, Welsh and Lind 1996). We believe that stream amphibians demonstrate strong potential as "sensitive species" (cf. Odum 1992), whose numbers can change relatively quickly in response to a range of environmental perturbations. Furthermore, use of streambed interstices by amphibians is a characteristic shared with early life stages of both resident and anadromous fishes, as well as many stream invertebrates. These other taxa, however, are either short-lived, explosive breeders, or subject to seasonal movements, all of which can complicate their use as bioindicators. Many species of stream-dwelling amphibians are highly philopatric, long-lived, and occur in relatively stable populations in undisturbed ecosystems. These attributes can make their relative numbers a useful and reliable indicator of environmental perturbations, both from known causes (Corn and Bury 1989, Blaustein et al. 1994b) and also possibly from causes that have yet to be identified (e.g., Corn and Fogleman 1984, Weygoldt 1989, Drost and Fellers 1996, Laurance 1996, Laurance et al. 1996, Pounds et al. 1997, Woolbright 1997, Lips 1998).

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APPENDIX

Definitions of primary mesohabitat types, pool sediment measures, and microhabitat attributes measured or estimated in association with belt samples.

Term	Definition
a) Mesohabitat attributes	
i) Primary mesohabitat types†	
All pools	Reaches with water depths from shallow to deep with evidence of scour. Cause of scour may be an obstruction, blockage, merging of flows, or constriction. This type includes main channel, lateral, backwater, and secondary channel pools. Flow velocities range from very low to swift. Substrate size is highly variable.
Run/glide	Wide shallow reaches flowing smoothly, with little surface agitation and no major flow obstructions. Velocities are low to moderate. These often appear as flood riffles. Typical substrates are gravel, cobble, and boulders.
Riffle	Shallow to moderately deep, swift, turbulent water. Amount of exposed substrate will vary. Substrates are usually cobble or boulder dominated.
Step run	A sequence of runs separated by short riffle steps. Substrates are usually cobble and boulder dominated.
Step pools	A sequence of pools separated by short riffle steps. Substrates are usually cobble and boulder dominated.
ii) Pool sediment measures	
Pool tail embedded	Visual estimate (percentage) of vertical surfaces of large substrates buried in fines and/or sand in pool tail.
Pool bowl sediment depth	Depth of sediment to the nearest tenth of a centimeter is taken at three points along the midline of the pool bowl. These measures are then averaged.
b) Microhabitat attributes	Measures and estimates of microhabitat attributes taken in association with amphibian sampling.
i) Aquatic conditions	
Proportion margin‡	Visual estimate (percentage) of channel composed of margin flow (percentage).
Proportion intermediate	Visual estimate (percentage) of channel composed of intermediate flow.
Proportion thalweg	Visual estimate (percentage) of channel flow composed of thalweg flow.
Flow margin	Flow rate in channel margin measured with a flowmeter in centimeters per second.
Flow intermediate	Flow rate in intermediate channel flow measured with a flowmeter in centimeters per second.
Flow thalweg	Flow rate in channel thalweg measured with a flowmeter in centimeters per second.
Canopy open‡	Measured by densiometer at center of the belt (percentage).
Water temperature	Measured by thermometer (°C).
Density of other Amphibians§	Density (captures per square meter) of the two other species of amphibians present in the belt.
ii) Cover estimates	Visual estimate of instream cover (percentage) in a series of categories.
Undercut banks‡	Overhang of stream banks, within 30 cm of water surface.
Woody debris‡	Woody debris of any size, including leaf litter overhanging water surface or underwater.
Riparian vegetation‡	Vegetation growing on the banks or in the stream. Must overhang within 30 cm of the water surface.
Large rock‡	Comprised of boulders and bedrock ledges. Only those portions that provide an overhang capable of hiding an amphibian are counted in this estimate.
Without covert ‡	Portion of the belt lacking any of the above cover types.
iii) Coarse aquatic substrates‖	Visual estimate of belt surface area comprised of coarse substrates (percentage) in the following categories.
Gravel	2.0-32.0 mm in diameter
Pebble	32.0-64.0 mm in diameter
Cobble	64.0-256.0 mm in diameter
Large rock	>256.0 mm in diameter and bedrock
Woody debris‡	Woody debris of any size and leaf litter. Must be in or surrounded by water.
Fine gravel volume	Proportion of mass of sediment sample taken at each belt (2.0-16.0 mm diameter).
Coarse gravel volume	Proportion of mass of sediment sample taken at each belt (16.0-32.0 mm diameter).
iv) Fine aquatic substrates ‖	
Embedded	Visual estimate (percentage) of vertical surfaces of large substrates buried in fines and/or sand in the belt.
Fines‡	Visual estimate (percentage) of belt surface area comprised of substrates <0.06 mm diameter.
Sand‡	Visual estimate (percentage) of belt surface area comprised of substrates 0.06-2.0 mm diameter.
Silt volume‡	Proportion of mass of sediment sample taken at each belt (samples are dried before sifting and weighing; <0.063 mm diam).
Sand volume‡	Proportion of mass of sediment sample taken at each belt (0.063-2.0 mm diameter).
Nonfilamentous algae	Visual estimate (percentage) of belt substrates covered by nonfilamentous algae growth.

†Modified from Hawkins et al. (1993).
‡Variable is transformed using arcsine to meet assumptions of normality.
§ Variable is transformed using natural log to meet assumptions of normality.
‖ Particle size based on Platts et al. 1983.